

Revision of the genus *Elzalia* Gerlach, 1957 (Nematoda: Xyalidae) including three new species from an oil producing zone in the Gulf of Mexico, with a discussion of the sibling species problem

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SYNOPSIS. The marine nematode genus *Elzalia* is revised and three new species, *Elzalia poli*, *E. federici* and *E. kima*, described from the oil producing zone of Campeche Sound in the Gulf of Mexico. *E. specularifer* (Timm, 1961) Hope & Murphy, 1972 and *E. tenuis* (Allgen, 1959) Gerlach & Riemann, 1973 are rejected as *spec. dub.* Pictorial & tabular keys to the genus are given. Some observations on the ecological and evolutionary significance of the genus are made.

INTRODUCTION

In 1986-88 samples of marine sediments were collected in the Campeche Sound, Gulf of Mexico, by the oceanographic vessel H-02 of the Mexican Navy, using Van Veen and Shipeck grabs. In 1986 eight samples were taken from near oil platforms in the Cayo Arcas region, the main loading point for oil tankers (Fig. 1, Table 1). More than 200 species of nematodes were extracted from the grey, jelly-like clay sediments in the samples, including three new species of *Elzalia*. This genus was absent in samples taken in 1987 from areas adjacent to the oil zone, but was present in samples collected from the Cayo Arcas region in 1988.

Table 1. Station localities (see Fig. 1)

Station	Latitude N	Longitude W	Depth (m)
1	21°00'	91°30'	37
2	20°30'	91°30'	30
3	20°20'	91°43'	37
4	20°11'	91°53'	42
5	20°07'	91°44'	37
6	20°00'	91°30'	31
7	19°45'	91°50'	53
8	19°25'	91°50'	42

This paper describes three new species of *Elzalia* from the Mexican samples. Pictorial and tabular keys to the genus are given, based on spicule and gubernaculum morphology. Some speculations on the zoogeography and the ecological and evolutionary significance of the genus are also made.

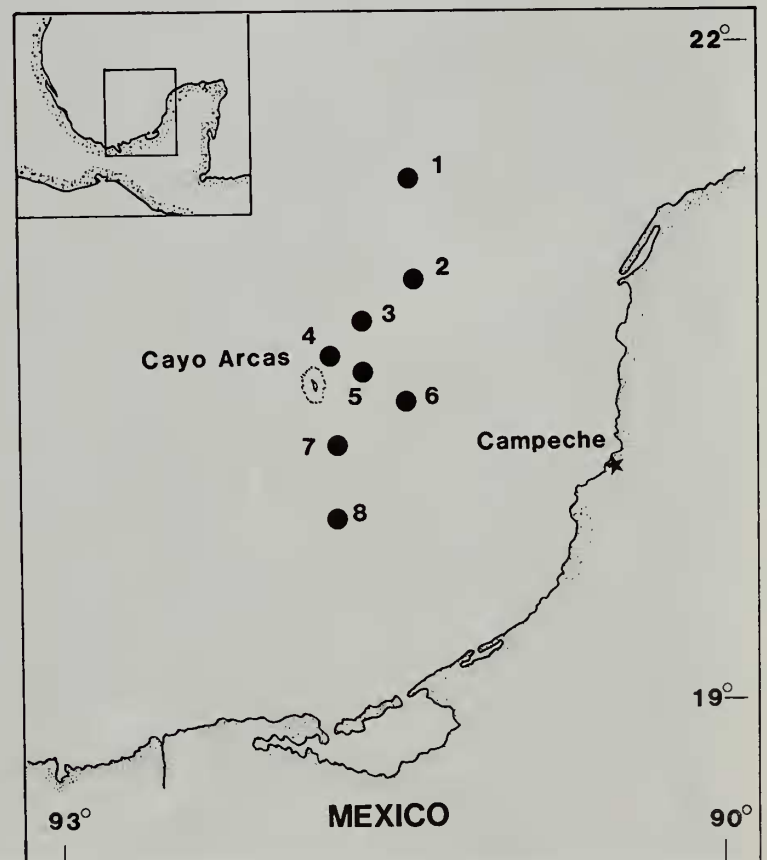


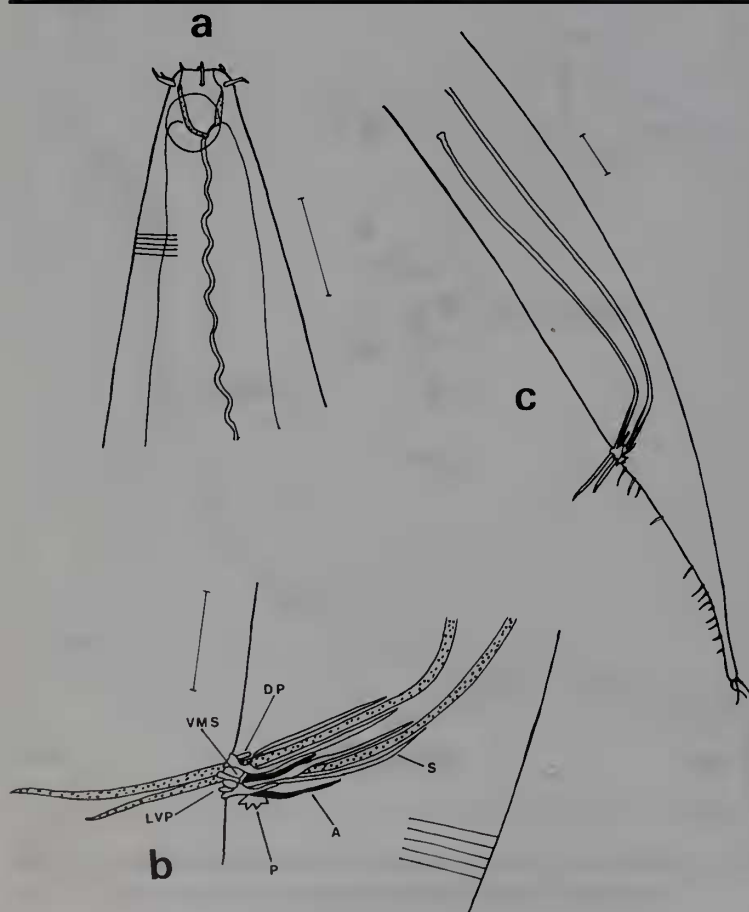
Fig. 1 Map of the Cayo Arcas region of the Gulf of Mexico showing sites from which *Elzalia* specimens were collected.

Table 2. Measurements of male specimens of *Elzalia poli*, *E. federici* and *E. kimaie* (all measurements in μm unless otherwise indicated).

	<i>E. poli</i>				Ef1 Holotype	Ef2	Ef3	<i>E. federici</i>			Ef6	Ef7	<i>E. kimaie</i>	
	Ep1 Holotype	Ep2 Paratypes	Ep3 Paratypes	Ep4 Paratypes				Ef4 Paratypes	Ef5 Paratypes	Ef6 Paratypes			Ek1 Holotype	Ek2 Paratype
Length (mm)	1.37	1.29	0.86	0.86	0.96	1.00	1.07	0.86	0.88	0.90	1.02	1.07	1.03	
Head width	13	15	12	11	11	11	12	11	11	14	12	12	12	
Maximum body width	86	83	47	43	56	56	50	28	56	50	58	64	58	
Anal body width	55	56	35	33	27	39	42	25	39	40	39	36	43	
Cephalic setae length	6	6	6	6	6	6	6	6	6	5	6	6	6	
Amphid distance from anterior	6	6	3	3	3	3	3	3	3	6	3	3	3	
Amphid width	11	10	8	8	10	6	11	6	8	9	10	7	7	
Buccal cavity length	14	14	13	17	13	14	14	13	15	13	14	11	12	
Buccal cavity width	8	9	8	6	6	6	6	6	8	8	8	8	9	
Oesophagus length	283	200	175	167	200	192	200	167	175	167	208	167	175	
Spicule length (arc)	300	333	128	150	124	242	235	117	133	107	133	75	69	
Tail length	175	167	116	154	118	133	128	125	125	120	133	133	128	
De Man ratios a	16	15	18	20	17	18	22	30	16	18	18	17	18	
b	5	6	5	5	5	5	5	5	5	6	5	6	6	
c	8	8	7	6	8	8	8	7	7	8	8	8	8	

Table 3. Measurements of female specimens of *Elzalia* (all measurements in μm unless otherwise indicated).

	E1	E2	E3	E4	E5	E6	E7	E8	E9
Length (mm)	1.28	1.13	1.13	0.92	1.13	1.00	1.02	1.08	0.98
Head width	17	14	12	11	14	14	11	11	11
Maximum body width	78	56	58	55	72	69	53	53	42
Anal body width	42	28	31	31	42	36	28	28	28
Cephalic setae length	7	6	6	6	8	7	6	6	6
Amphid distance from anterior	3	4	3	4	5	4	4	4	6
Amphid width	12	8	12	8	8	9	8	10	9
Buccal cavity length	17	13	16	17	15	11	14	14	14
Buccal cavity width	8	8	7	6	9	8	4	6	6
Oesophagus length	208	200	200	167	208	208	208	208	183
Vulva distance from anterior	181	167	158	125	142	158	133	142	125
Tail length	633	592	558	492	583	517	533	558	450
De Man ratios a	17	20	19	17	16	14	19	20	24
b	6	6	6	6	5	5	5	5	5
c	7	7	7	7	8	6	8	8	8
V%	49	53	50	54	53	52	53	52	46



TAXONOMY

Generic diagnosis

Xyalidae. Spindle shaped colourless worms. No pigment spots or ocelli in preserved specimens. Cuticle finely, transversely striated. Buccal cavity prominent, cylindrical, cuticularized. Amphids large, circular or oval, granular in appearance, indistinct. Six labial papillae (R1), ten cephalic setae (R2 + R3). Somatic setae irregularly found, sometimes prominent ventral caudal setae, 3 distinct terminal setae. Oesophagus narrow anteriorly, widening posteriorly. Bulb absent. Spicules often long, slender. Gubernaculum often complex. Single anterior, outstretched testis, subventral right of intestine. Single anterior, outstretched ovary, lateral left of intestine. Tail conico-cylindrical, slightly clavate.

Remarks

Elzalia specimens showed few reliable specific characters, intraspecific morphometric variation seemed to be as large as

Fig. 2 *Elzalia poli*, holotype: (a) anterior, scale bar = $20\mu\text{m}$; (b) gubernaculum and distal parts of spicules (black shading = dorsally directed apophyses, stippling = spicules, see text for explanation of labels), scale bar = $20\mu\text{m}$; (c) posterior showing spicules, scale bar = $30\mu\text{m}$.

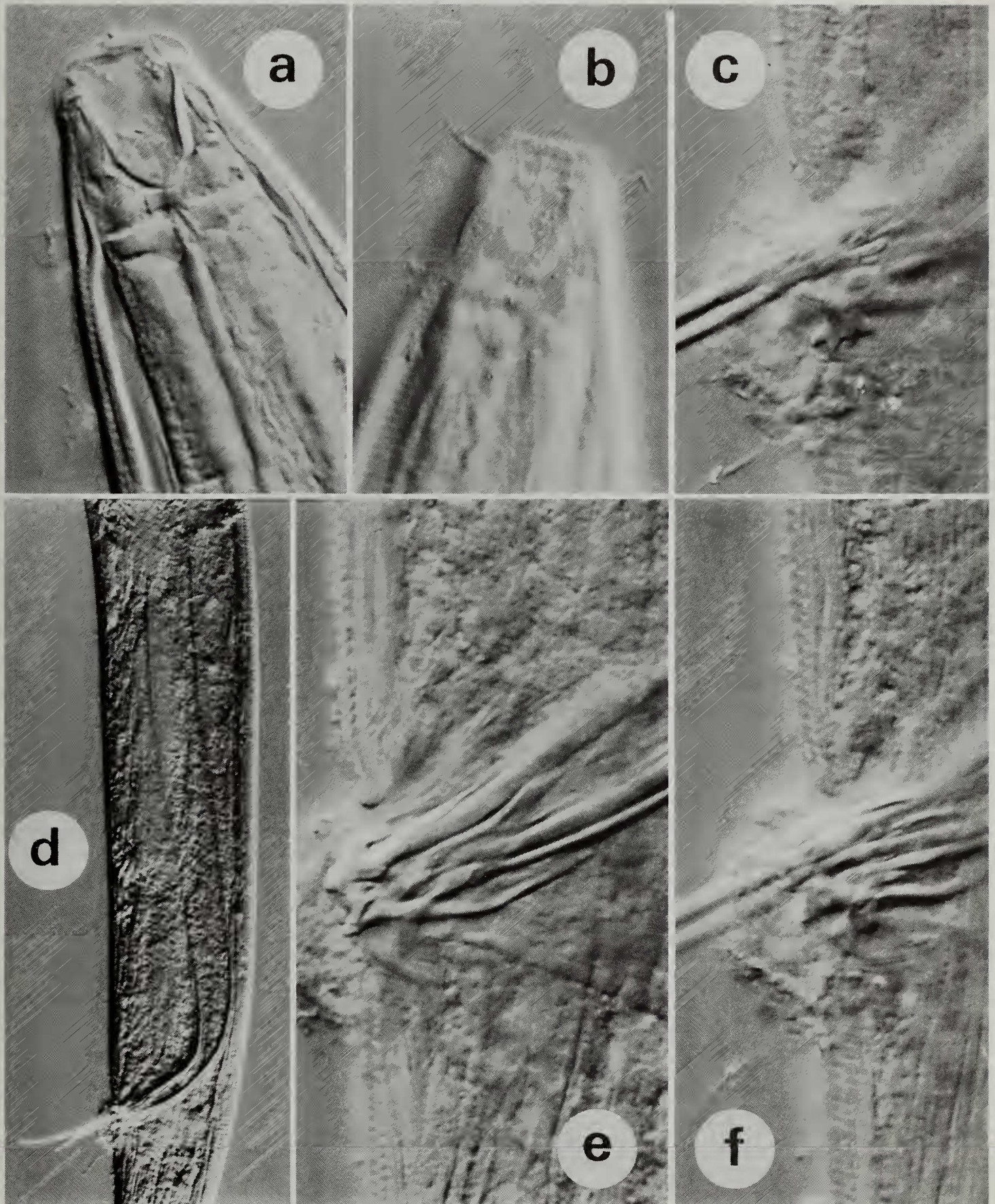


Fig. 3 *Elzalia poli*, holotype: (a) head showing buccal cavity; (b) head showing amphid and cephalic setae; (c) gubernaculum showing posteriorly directed 'leaf-like' projection; (d) spicules; (e) gubernaculum showing dorsal projections, spicule sheaths and dorsally directed apophyses; (f) same view as 'e', but at the focal plane of the spicules. 100 × objective used except 'd', 20 ×.

interspecific variation among males of the three new species. The possible exception was *E. mediterranea*, which was smaller than the other species. The body/spicule length ratio proved useful in distinguishing *E. kima* (Table 4). The best character for distinguishing species proved to be spicule and gubernaculum morphology (see pictorial key, Fig. 9). The gubernaculum was often extremely complex and, although difficult to interpret, provided characters for specific diagnosis. No reliable characters to distinguish females and juveniles of different species were found.

Figure 6 of *E. kima* shows a kink in the wall of the buccal cavity giving the appearance of a two chambered mouth. This was not a specific character as it appeared occasionally in some specimens of the other two species.

Lorenzen (1981) cited the position of the anterior gonad (to the left of the intestine) as the holapomorphic (synapomorphic) character which separates the Xyalidae within the Monhysteroidea. The location of the testis in *E. poli* and *E. federici* (and presumably other species in the genus) would seem to contradict Lorenzen's observation. Two other species were reported by Lorenzen to have anterior gonads on the right, *Hofmaenneria niddensis* and *Steineria pilosa*. The situation is further complicated in *Elzalia* because where the position of the ovary could be determined, it was on the left. Lorenzen (1979) reported that males and females of a species almost always show conformity in gonad position. He cited few exceptions (mostly involving species with one testis and two ovaries) none of which come from the Xyalidae. We hesitate to over-interpret this information because flattening meant that gonad position could be determined accurately in only a few specimens.

DESCRIPTIONS OF NEW SPECIES

The new species were described using male specimens. Females could not be determined and so are described *en bloc*.

Specimens were flattened by the mounting method so maximum widths are probably exaggerated and 'a' ratios underestimated. Measurements are given in Tables 2 & 3. Flattening also made it difficult to determine the lateral position of the gonads relative to the intestine.

Type material was deposited in the British Museum (Natural History).

Elzalia poli sp. nov.

(Figs 2 & 3)

MATERIAL STUDIED. Holotype: Ep1, BM(NH) 1989.1.2. Paratypes: Ep2 & Ep3, BM(NH) 1989.1.3; Ep4, BM(NH) 1989.1.7. ('Ep' nos identify individual specimens, see Table 2). All males.

LOCALITY: Ep1–3—Station 4; Ep4—Station 6. Specimens that were not used in this study were also found at Stations 1 and 2 (see Fig. 1).

DESCRIPTION. The morphological complexity of the gubernaculum gave rise to a distinct shape, albeit one with structures common to other members of the genus, which could be divided into four sections. The first was the ventral main section (VMS). This completely enclosed the spicules (with a possible anterior gap?) and was made up of a series of lateral

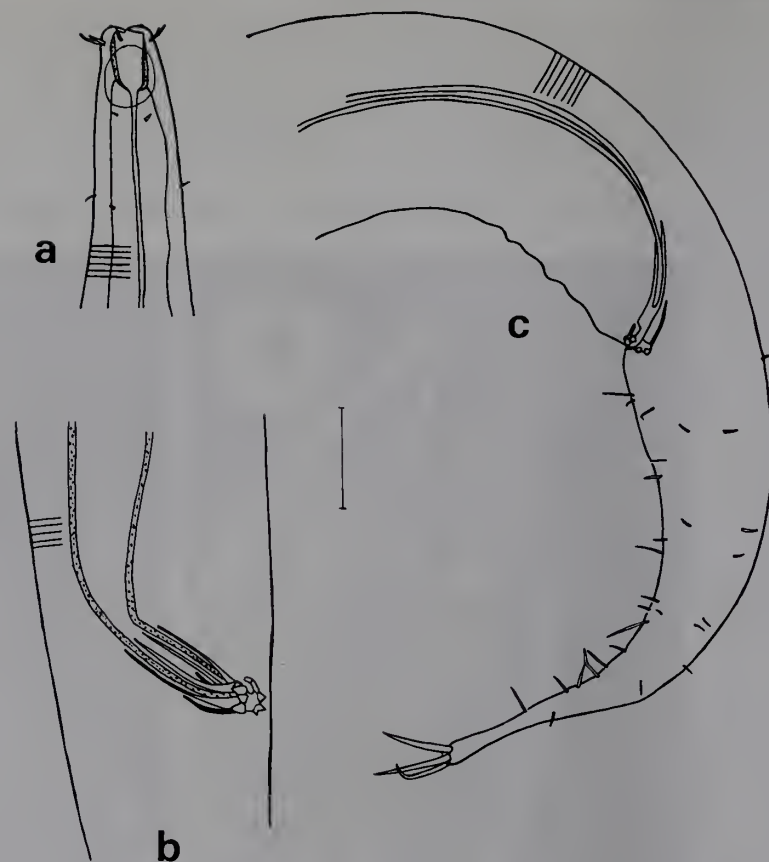


Fig. 4 *Elzalia federici*. Holotype: (a) anter or; (c) posterior (shading = dorsally directed apophysis). Paratype (Ef3): (b) gubernaculum with distal end towards observer, note 'finger-like' projections. Scale bar = 20µm.

and ventral projections (LVP) like the spikes on a mace, and a pair of dorsal projections (DP) anteriorly which gave the impression of two backward pointing hooks. The second section consisted of sheaths (S) extending along the spicules. Observations on a number of *Elzalia* males from different species suggested that the long thin spicules were protruded and withdrawn along these sheaths which act as 'guide rails'. The third section consisted of two slender, dorsally directed apophyses (A). The fourth was a pair of posteriorly directed 'leaf-like' projections or plates (P) which had four distinct triangular endpoints, two pointing posteriorly, one dorsally and one ventrally in most specimens (one had only 3 points). The spicules were long and slender. In one specimen (Ep4) the testis could be determined as subventral right of the intestine. Excretory pores and nerve rings were not observed.

DIFFERENTIAL DIAGNOSIS. *Elzalia poli* sp. nov. could be distinguished from *E. mediterranea* Vitiello, 1971, by the simple gubernaculum and short body length (573µm) found in the Mediterranean species. *E. poli* is closely similar to the type species *E. floresi* Gerlach, 1957. The gubernaculum in *E. floresi* is simpler, with no lateral and only one ventral projection.

REMARKS. Gerlach's specimen could be interpreted as having a gubernaculum essentially similar to the new species. It contained all four elements, in particular the four pointed posteriorly directed 'leaf-like' projections. The main section had one ventral projection and a structure that might be interpreted as an anterior 'hook'. The hypothesis that the new specimens were conspecific with *E. floresi* was considered and rejected because of (a) the simpler morphology of the latter's gubernaculum and (b) the large distance between the two localities (Southern Brasil and Mexico), which are separated by the Amazon estuary. However, further work along the

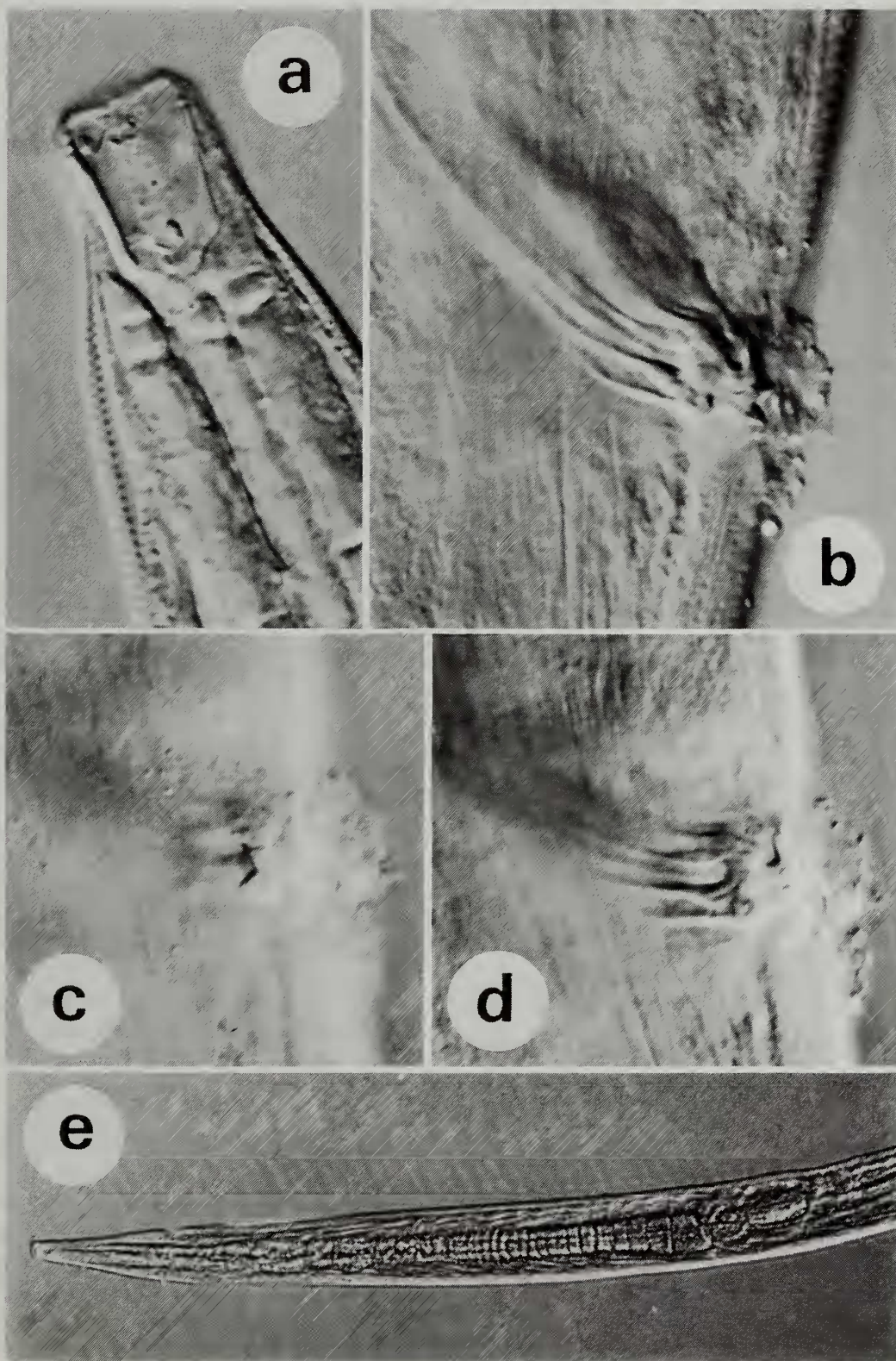


Fig. 5 *Elzalia federici*, paratype: (a) head showing buccal cavity; (b) gubernaculum (c.f. Fig. 4b); (c) distal end of gubernaculum showing 'finger-like' projections; (d) gubernaculum showing dorsal projection. *Elzalia* female (E3): (e) anterior showing ovary. 100 × objective used except 'e', 10 ×.

South American tropical coastline may indicate that intermediate forms exist in which case the two names might be synonymized.

***Elzalia federici* sp. nov.**

(Figs 4 & 5)

MATERIAL STUDIED. Holotype: Ef1, BM(NH) 1989.1.6. Paratypes: Ef2, BM(NH) 1989.1.1; Ef3, BM(NH) 1989.1.4; Ef4, BM(NH) 1989.1.5; Ef5, BM(NH) 1989.1.8; Ef6, BM(NH) 1989.1.3; Ef7, BM(NH) 1989.1.9 ('Ef' nos identify individual specimens, see Table 2). All males.

LOCALITY. Ef1 & Ef8—Station 8; Ef2 & Ef6—Station 4; Ef3—Station 6; Ef4—Station 7; Ef5—Station 3. Specimens not used in this study were also found at Stations 1 and 2 (see Fig. 1).

DESCRIPTION. *Elzalia federici* was closely similar to *E. poli* except for gubernaculum shape. Principally, it lacked the posteriorly directed 'leaf-like' projections and the ventral main section was less complicated with finger-like projections on the left and right side of the distal part.

DIFFERENTIAL DIAGNOSIS. *Elzalia federici* sp. nov. is most similar to *E. poli* sp. nov. and *E. floresi* Gerlach, 1957 in size and general morphology but is distinguished by the absence of posteriorly directed 'leaf-like' projections on the gubernaculum. It can also be distinguished from *E. mediterranea* Vitiello, 1971 by the simpler gubernaculum and smaller body length described by Vitiello.

REMARKS. The close similarities between *E. federici* and *E. poli* and their presence in the same location suggested that they might be a single species exhibiting either (a) phenotypic variation or (b) apparent differences caused by functional morphology (eg. whether the spicules were protruded or retracted). However, no correlation was observed between gubernaculum appearance and any other factor (such as spicule position). Also the two shapes were always discrete, no intermediates were found. We, therefore, reject the hypothesis that they are conspecific. In a single specimen (Ef4) the single, anterior testis could be determined as subventral right of the intestine.

***Elzalia kima* sp. nov.**

(Figs 6 & 7)

MATERIAL STUDIED. Holotype: Ek1. Paratype: Ek2. BM(NH) 1989.1.4. ('Ek' nos identify individual specimens, see Table 2). Both males.

LOCALITY. Station 6 (see Fig. 1).

DESCRIPTION. The gubernaculum was simpler than the other new species described here but it showed the same basic morphology. The ventral main section lacked the spikes or finger-like projections described earlier and did not wrap around the spicules so completely but possessed a pair of posteriorly directed 'leaf-like' projections which ended in four posteriorly directed points. The sheaths extending along the spicules had thin dorso-ventral alae but spicules were shorter and stouter in this species. Lateral position relative to the gut of the single, anteriorly directed, ventral, testis could not be determined.

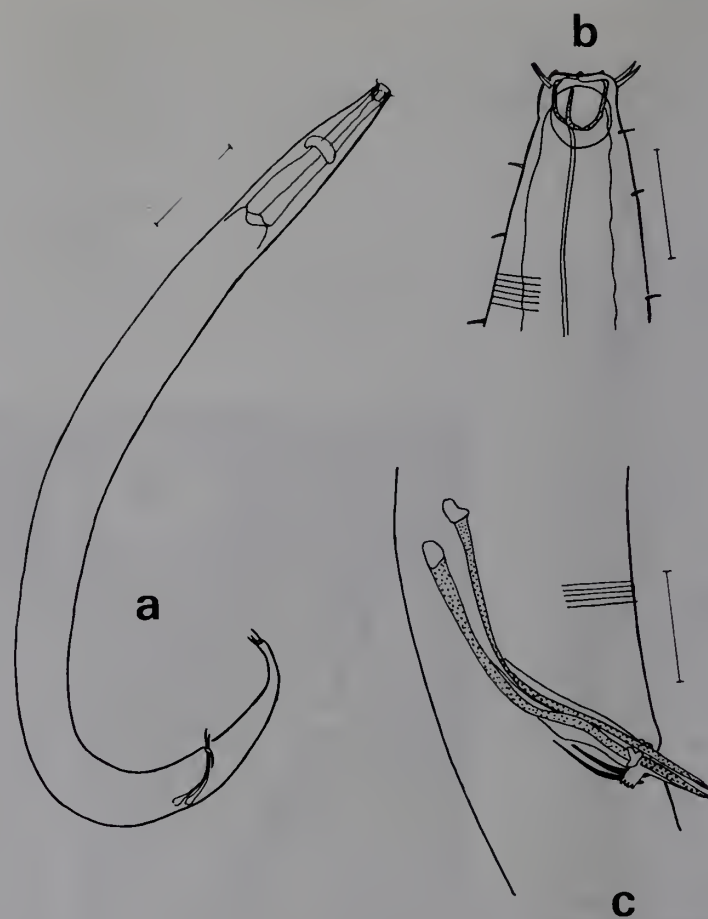


Fig. 6 *Elzalia kima*, holotype: (a) whole animal, scale bar = 100µm; (b) anterior, scale bar = 20µm; (c) spicules and gubernaculum (shading as Fig. 2), scale bar = 20µm.

DIFFERENTIAL DIAGNOSIS. *Elzalia kima* was distinguished from all other species of *Elzalia* by short stout spicules giving a high body length/spicule length ratio. *E. mediterranea* Vitiello, 1971, had a similar absolute spicule length to the new species but note that *E. mediterranea* was small so the body length relative to spicule length was low in this species (Table 4).

Female specimens

(Figs 7 & 8)

MATERIAL STUDIED. E1, BM(NH) 1989.1.5; E2, BM(NH) 1989.1.7; E3, BM(NH) 1989.1.10; E4, BM(NH) 1989.1.11; E5, BM(NH) 1989.1.12; E6, BM(NH) 1989.1.13; E7, BM(NH) 1989.1.14; E8, BM(NH) 1989.1.15; E9, BM(NH) 1989.1.16 ('E' nos identify individual specimens, see Table 3).

LOCALITY. E1 & E9—Station 7; E2, E3 & E5—Station 6; E4—Station 5; E6–8—Station 8 (see Fig. 1).

DESCRIPTION. Females were similar to the males of the three species in body characters. All had a single, anteriorly-directed, outstretched, ovary. In some specimens gonad position relative to the intestine could be reliably determined as lateral left. Sperm was occasionally observed in the variably sized post-uterine sac. Caudal glands were present and nerve rings were often observed.

Generic keys

Two tabular keys, one pictorial, to the valid species of the genus *Elzalia* are presented, Table 4 and Fig. 9.

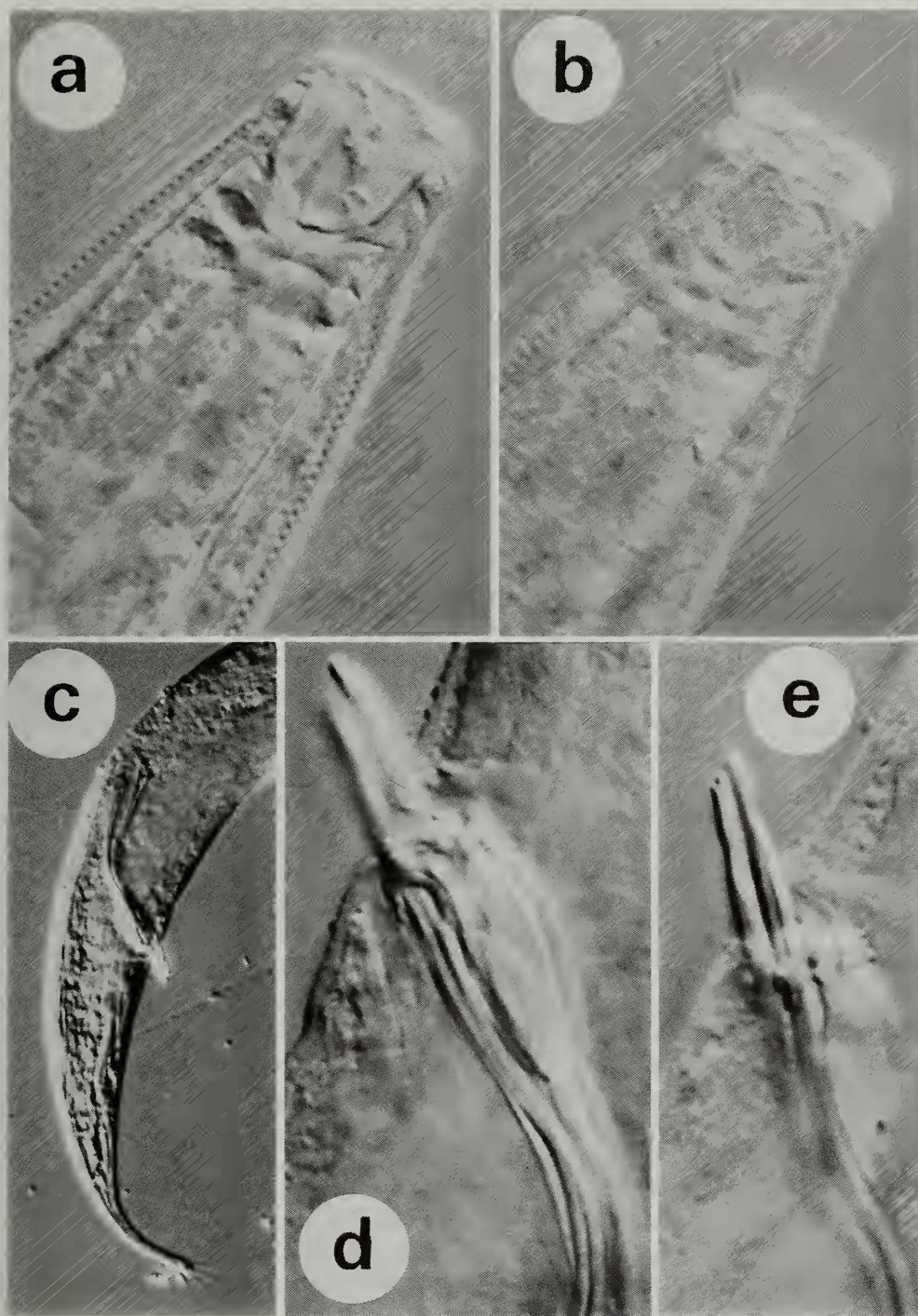


Fig. 7 *Elzalia kima*, holotype: (a) head showing buccal cavity; (b) head showing amphid and cephalic setae; (c) posterior showing spicules and tail; (d) gubernaculum showing dorsal projections; (e) gubernaculum showing posteriorly directed 'leaf-like' projection. 100 × objective used except 'c', 20 ×.

Table 4. Tabular key to the species of the genus *Elzalia*

Species	length (mm)	Spicule arc length (mm)	length/spicule length ratio
<i>E. federici</i>	0.86–1.07	107–242	4.1– 8.4
<i>E. floresi</i>	1.04	170	6.1
<i>E. kima</i>	1.03–1.07	69– 75	14.3–15
<i>E. mediterranea</i>	0.57	35	16.3
<i>E. poli</i>	0.86–1.37	128–333	3.9– 6.7

Gut contents

Diatoms were discovered in the guts of many specimens examined and in the intestine of a *Trichotheristus* specimen collected at the same time, together with a gubernaculum of *E. poli*.

Zoogeography

Elzalia was erected by Gerlach (1957) for *E. floresi* (type species) from the Sao Paulo region of the southern coast of Brasil. Vitiello (1971) described a new species from the Mediterranean, *E. mediterranea*. Hope & Murphy (1972) synonymised *Megalolaimus* Timm, 1961, transferring *M. speculifer* to *Elzalia*. Timm's description was of a solitary female but the current study (see below) suggests that only males can reliably be used to describe *Elzalia* species. It seems most unlikely that Timm's species could be recognised again with any certainty so it is here declared a *spec. dub.* However, the specimen was almost certainly *Elzalia* so the zoogeographic record of a member of this genus from the Bay of Bengal stands. Gerlach & Riemann (1973; see also Gerlach, 1963), transferred *Filipjeviella tenuis* Allgen, 1959, to *Elzalia*. This species was also described from a single female so is here considered *spec. dub.* But the description

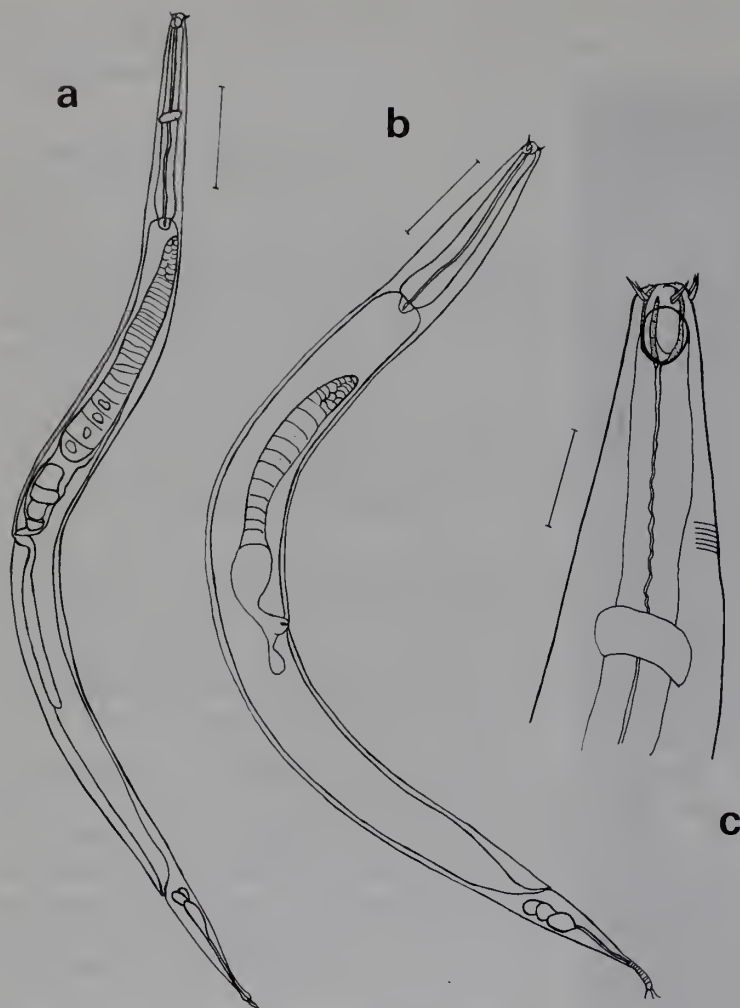


Fig. 8 *Elzalia* females: (a) whole body (EB), note large post-uterine sac, scale bar = 100 μ m; (b) whole body (E5), note small post-uterine sac, scale bar = 100 μ m; anterior (E4), scale bar = 20 μ m.

was weak and it is not certain to which genus the specimen belonged. For example, from the figure it appeared to have four cephalic setae. This specimen was collected from the Antarctic, unlike all other *Elzalia* records which are from warm waters (Bay of Bengal, Brasil, Gulf of Mexico, Mediterranean). This zoogeographic record should therefore be considered doubtful.

EVOLUTIONARY AND ECOLOGICAL IMPLICATIONS

The three new species described pose two questions. Of the five known *Elzalia* species why do we find three species so similar co-existing in the same area at the same time? Why do the males have such complicated cuticularized reproductive structures when the species are otherwise so similar that females are indistinguishable?

That large number of nematode species can be found apparently co-existing is a common observation (Platt & Warwick, 1980). Three or more species from one genus can apparently co-exist, eg. Lamshead (1986) surveyed a low-water spring tide, fine sand habitat at a specific time in the Clyde inland-sea area and found nine genera (out of 69, i.e. 13%) with three or more species present. Globally, nematodes exhibit enormous speciation, May (1988) estimates that

nematodes and insects have in excess of one million species each. The figure of 4000 species of described marine nematodes (Platt & Warwick, 1980) is almost certainly a substantial underestimate because it is based mostly on studies in shallow temperate seas in the northern hemisphere. Deep-sea and tropical waters are richer in nematode species, most new to science (pers. obs.). This richness of nematode species is an anomaly for deterministic equilibrium ecology, particularly the co-existence of so many similar animals in, what appears to be, a homogeneous environment. This problem is usually explained in terms of resource partitioning by nematode species either by locomotion, or by morphological or physiological specialisation (Platt & Warwick, 1980).

Jensen, 1988, reported four *Acantholaimus* species co-existing in the Arctic deep sea. They had different buccal cavity morphologies which Jensen considered evidence of food resource partitioning. But such a situation is exceptional, *morphologically* similar co-existing species, as in *Elzalia*, represent the norm; hence Tietjen & Lee's (1977) speculation of *physiological* resource partitioning. In the Clyde survey (*op. cit.*) four species of *Neochromadora* were discovered, of which three were morphologically similar; while females and juveniles of the two *Leptolaimus* species were so similar that they could be distinguished only with great difficulty. If a non-deterministic, disturbance-controlled, or a deterministic chaos view of ecology is postulated then co-existence of similar species ceases to be an ecological problem but remains an evolutionary one. Assuming number of species is an indication of rate of speciation (Sanders & Grassle, 1971) then nematodes display high speciation rates. Jablonski & Lutz (1983) and Hansen (1978) found paleontological evidence that benthic invertebrate species with high dispersal rates (associated with pelagic larvae) have low extinction and speciation rates. Nematodes, which have conservative reproductive strategies, should have high extinction and speciation rates due to localization and vicariance events. This assumes that a conservative reproductive strategy is indicative of low dispersal rates. Such an assumption is reasonable but not necessarily true.

Closely related species co-existing, as in many marine nematode genera, implies effective reproductive barriers. Nematodes have complicated reproductive apparatus, especially in males. Such characters are important in a number of vertebrate and invertebrate taxa (Arnold, 1986). We may speculate on resemblances between nematode male reproductive structures and the 'key-lock' mechanisms found in taxa such as arthropods and lizards as a way of ensuring reproductive isolation between closely related, co-existing nematode species.

Finally, it is difficult to reconstruct phylogenies in a group with high rates of speciation and extinction due to both the loss of intermediate character states and high levels of homoplasy. Lorenzen (1981) produced a meticulously thorough phylogenetic reconstruction of the group. Nevertheless, even limited studies of warm water genera such as this revision of *Elzalia* produce exceptions to his cladogram and it is likely that further studies in tropical and deep-sea habitats will reveal greater problems.

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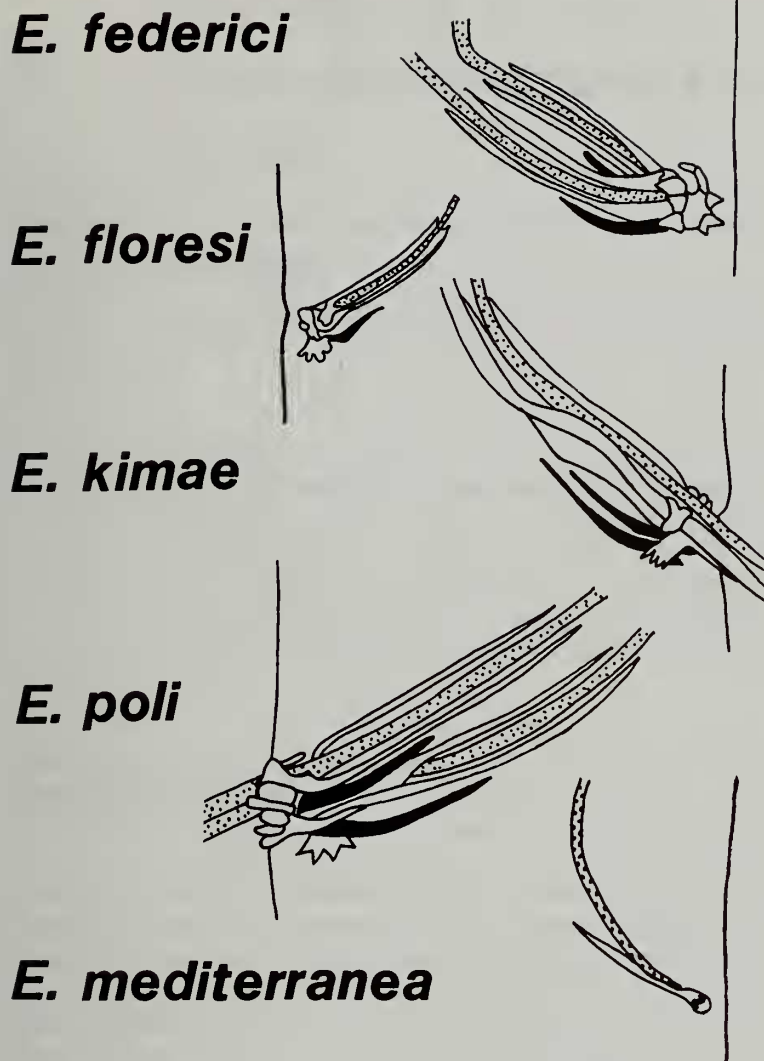


Fig. 9 Pictorial key to the genus *Elzalia* based on the morphology of the gubernaculum. All drawings are to scale (shading as Fig. 2).

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